

*VARIABLE-INTERVAL REINFORCEMENT SCHEDULE VALUE INFLUENCES
RESPONDING FOLLOWING REM SLEEP DEPRIVATION*

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The effects of rapid-eye movement sleep deprivation (REMSD) in rats were studied in relation to variable-interval (VI) reinforcement schedule value. Initially, lever pressing was maintained on a VI 30-s schedule of food pellet delivery. After a baseline was established, rats were repeatedly exposed to 96 hr of REMSD and control conditions of an equivalent duration. Responding decreased following REMSD but not after exposure to control conditions. Lever pressing was then maintained on a VI 15-s schedule of food pellet delivery and exposure to the REMSD and control conditions was repeated. Under this condition following repeated REMSD exposures, rates of lever pressing became similar to baseline responding. A VI 30-s schedule of food pellet delivery was then reinstated and REMSD and control conditions were repeated. Lever pressing following exposure to the REMSD condition decreased for 3 of 4 rats. Results suggest that VI schedule value influences the effects of REMSD on responding.

Key words: sleep deprivation, positive reinforcement, schedule-dependent, reinforcement density, variable interval, lever pressing, rat

Sleep has a pervasive effect on waking behavior. The most striking example of the importance of sleep is that its prolonged absence is fatal in humans and nonhumans (Gallassi et al., 1996; Rechtschaffen, Gilliland, Bergmann, & Winter, 1983). Sleep influences a wide range of psychological processes, including attention, remembering, affect, and emotion (Maquet, 2001). The most prevalent strategy for studying how sleep relates to waking behavior is the use of sleep deprivation. Using this approach, researchers selectively deprive subjects of sleep and analyze changes in behavior that occur as a function of sleep deprivation (Walsh & Lindblom, 1997).

The majority of research on sleep deprivation has focused on acquisition and memory, particularly the role of sleep deprivation on the establishment of stimulus control (Hobson & Pace-Schott, 2002; Smith, 1996). Less research attention has been given to how sleep deprivation affects basic parameters of operant behavior such as responding maintained by schedules of positive or negative re-

inforcement. Recent research shows that rapid-eye movement sleep deprivation (REMSD) increases responding on free-operant avoidance tasks (Kennedy, 2000; Kennedy, Meyer, Werts, & Cushing, 2000; Smith & Kennedy, 2003). For example, Kennedy et al. (2000) established baseline performances on a free-operant avoidance procedure and then repeatedly exposed individual rats to 24, 48, or 96 hr of REMSD. Response rates increased by approximately 50% following 48 hr of REMSD, with little or no change observed for the other sleep deprivation exposures. The findings of Kennedy and his colleagues have shown that 48 hr of REMSD does not change the percentage of shocks avoided for proficient responders, but response rates increase as a monotonic function of baseline lever pressing via increases in brief interresponse times (IRTs).

The findings of Kennedy et al. (2000) raise the question of whether changes in behavior are due to an overall increase in responding across a variety of behavioral processes or whether the effects of REMSD are selective for negatively reinforced responding. To further explore this question, Kennedy (2002) established lever pressing on a multiple fixed-interval (FI 60 s) fixed-ratio (FR 30) schedule of appetitive reinforcement. Rats were then repeatedly sleep deprived for 24, 48, or 96 hr. REMSD exposures of 24 or 48 hr had no effect on responding for any of the rats, but 96

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hr of REMSD decreased responding on both FI and FR components of the multiple schedule of all 4 rats. Although responding increased following repeated exposures to 96 hr of REMSD, responding was not affected by lesser amounts of sleep deprivation.

The findings of Kennedy et al. (2000) suggest that (a) the effects of REMSD differ for negatively versus positively reinforced responding, and (b) that responding may be sensitive to competition between sleep deprivation and food deprivation. This latter observation suggests that response allocation may shift from food to sleep under certain circumstances. For example, as sleep deprivation is increased (e.g., 96 hr as in Kennedy, 2002) and food restriction is held constant, response allocation might shift from food-reinforced responding to sleeping. Or, as rate or amount of reinforcement is increased and sleep deprivation is held constant, response allocation might shift away from sleep and toward food-reinforced responding. This observation suggests the importance of taking into account multiple establishing operations when examining the operant effects of sleep deprivation. In our previous research, we have shown extreme sleep deprivation can induce a shift in response allocation away from food-reinforced responding, but we have not tested the possible effects of reinforcer density on changes in response allocation.

In the current experiment, we sought to determine if positively reinforced responding might be sensitive to the rate of reinforcement under constant sleep deprivation levels. We studied whether two different schedules of food reinforcement would influence behavior following 96 hr of REMSD. Rats were first tested on a variable-interval (VI) 30-s schedule of food pellet delivery with and without REMSD, then the schedule was changed to a VI 15-s schedule and, finally, the VI schedule was returned to 30 s. The experimental question was whether the effects of REMSD would be greater under the VI 30-s schedule versus the VI 15-s schedule. Such an experimental manipulation allows for a test of how sleep deprivation may influence response allocation to food-reinforced behavior.

METHOD

Subjects

Subjects were 4 experimentally naive Sprague-Dawley male rats (R32, R33, R40,

and R41), obtained from Harlan, Inc., and individually housed with ad libitum access to water. At the start of the experiment the rats were approximately 120 days old and weighed 400 g. Each rat's weight was maintained between 400 g and 425 g throughout the experiment by restricting extra-session food intake. A 12:12 hr light/dark cycle was in effect (with light onset occurring at 6:00 a.m.). Experimental sessions occurred between 10:00 a.m. and 11:00 a.m. each day, 5 days per week during the lights-on period.

Apparatus

Standard operant conditioning chambers (MED Associates, Inc.), 24 cm wide, 30.5 cm long, and 29 cm high, were used. Each chamber was housed in a MED Associates sound-attenuating enclosure. Chambers consisted of translucent plastic side panels with aluminum rear and instrument panels. Each instrument panel contained two nonretractable levers (in the left and right lower corners of the panel, respectively), a pellet receptacle (located at the bottom of the panel between the levers), and a houselight (located at the center top of the panel). The levers extended 2.2 cm from the panel wall, were 2.2 cm wide, and required a minimum downward force of 0.25 N. The pellet receptacle extended 1 cm from the panel wall and was 0.8 cm wide and 0.8 cm deep. An electromechanical 28-V DC pellet dispenser (MED Associates ENV-203) provided 45-mg Noyes food pellets (improved Formula A). The houselight was a 28-V DC bulb located within a chrome-plated holder. Floors consisted of 19 stainless steel rods (4.8 mm in diameter, spaced 1.6 cm apart). White noise generators supplied 80-dB sound to the experimental room. All events in the operant chamber were controlled by MED Associates software (MED-PC® version 2.0) operating on a MSDOS-based personal computer.

REMSD was accomplished using the pedestal-over-water method (Morden, Mitchell, & Dement, 1967). REMSD tanks were cylindrical containers, 1 m high and 0.5 m wide. Two platforms were placed in each tank. Each platform measured 7.5 cm in diameter and was positioned 9 cm from other platforms and the tank wall. The top of each platform was raised 1 cm above 15 cm of water (see Figure 1).



Fig. 1. Rapid-eye movement sleep deprivation apparatus. A rat was singularly housed in the apparatus by placing it on a platform that was situated above the water and below a wire mesh screen that allowed access to food and water.

Procedure

Each session began with houselight illumination that was continuous unless otherwise noted. Lever presses to obtain a food pellet were shaped by successive approximations (right lever presses for R33 and R41; left lever presses for R32 and R40). Initially, each lever press resulted in food pellet delivery. Training sessions lasted until 80 lever presses occurred or 20 min elapsed. Training continued until lever pressing occurred 80 times during a session for three consecutive sessions (M sessions = 4.5; range, 4 to 6). Following lever-press shaping, rats completed a 10-min session in which a VI 5-s reinforcement schedule was operative. This and all subsequent VI schedules were generated by procedures described by Hoffman and Flescher (1962). VI schedule values were increased by 5 s every three to six sessions until a terminal schedule of VI 30 s was reached. Between 17 and 31 sessions ($M = 23.3$) were required before the VI 30-s schedule was introduced.

Baseline. After changing to the VI 30-s schedule, three 10-min VI 30-s components

were added to each session and three 1-min blackouts separated the four VI components. During blackouts, houselight illumination was off and lever pressing produced no consequences. A single four-component baseline session was conducted each day. Baseline response rates were judged to be stable when the final two components were within $\pm 10\%$ of the mean of the previous 10 baseline sessions (final two components per session). Rats required between 52 and 56 sessions to meet this stability criterion ($M = 54.3$). Once the stability criterion was met the rat was exposed to REMSD or control conditions.

REMSD and control conditions. After a baseline session in which the stability criterion was met, a rat was exposed to a cage-control (CC), REMSD, or tank-control (TC) condition for 96 hr (with no testing occurring during this time period). The REMSD exposure entailed placing a rat in the REMSD apparatus (see Figure 1). Because the REMSD condition differed from baseline in that rats were (a) placed in an aquatic setting and (b) withheld from daily baseline sessions, two control conditions were used. The TC apparatus was identical to the REMSD tank, except that two 15-cm diameter pedestals replaced the 9.5-cm pedestals. The TC condition exposed rats to the possible stress effects of the aquatic setting, but allowed ad libitum access to sleep because of the larger pedestals (see Smith & Kennedy, 2003). The CC condition exposed rats to the same postponement of baseline sessions as REMSD and TC conditions without being placed in an aquatic setting. The CC condition consisted of maintaining a subject in its vivarium cage. During CC, REMSD, and TC conditions, rats had ad libitum access to fresh water and were maintained on their food restricted diets.

REMSD and control conditions were randomized within blocks of CC, REMSD, and TC exposures for each rat (see Table 1). Immediately following exposure to REMSD or control condition, rats were exposed to a single test using the four-component VI 30-s schedule of reinforcement at the same time of day as baseline sessions. Table 2 shows the mean number of baseline sessions between individual CC (inter-CC), REMSD (inter-REMSD), and TC (inter-TC) condition exposures. Table 2 shows that for each rat the amount of time that elapsed between expo-

Table 1

Sequence of Cage Control (CC), REM Sleep Deprivation (REMSD), and Tank Control (TC) Conditions.

Reinforcement schedule	Rat			
	32	33	40	41
VI 30-s	TC	REMSD	REMSD	CC
	REMSD	TC	TC	REMSD
	CC	CC	CC	TC
	REMSD	REMSD	REMSD	TC
	TC	TC	TC	REMSD
	CC	CC	CC	CC
	CC	TC	TC	REMSD
	TC	REMSD	REMSD	TC
	REMSD	CC	CC	CC
VI 15-s	TC	REMSD	REMSD	CC
	REMSD	TC	CC	TC
	CC	CC	TC	REMSD
	CC	REMSD	TC	TC
	TC	CC	REMSD	REMSD
	REMSD	TC	CC	CC
	TC	CC		CC
	REMSD	TC		TC
	CC	REMSD		REMSD
				TC
VI 30-s	REMSD	TC	TC	TC
	CC	REMSD	REMSD	REMSD
	TC	CC	CC	CC
	CC	CC	REMSD	REMSD
	REMSD	TC	CC	CC
	TC	REMSD	TC	TC
	TC	TC	CC	CC
	CC	CC	TC	TC
	REMSD	REMSD	REMSD	REMSD

tures to a particular type of condition (e.g., REMSD) was consistent throughout the experiment. Following exposure to a CC, REMSD, or TC condition and subsequent behavioral test (see baseline), a rat was returned to its vivarium cage and daily baseline sessions were reestablished. Once baseline stability was reestablished, the rat was then exposed to another REMSD or control condition.

VI schedule values. Following repeated exposures to the CC, REMSD, and TC conditions (see Table 1), the baseline schedule of reinforcement was changed to VI 15 s. This change established a four-component VI 15-s schedule of reinforcement procedure that was identical to the previous VI 30-s procedure except for the interval value. Sessions were conducted until the baseline stability criterion was met for a rat and required between 43 and 72 sessions ($M = 51$). A rat was then

Table 2

Sessions Between Individual Cage Control (Inter-CC), REM Sleep Deprivation (Inter-REMSD), and Tank Control (Inter-TC) Conditions.

Condition	Rat			
	32	33	40	41
Inter-CC				
Mean	46.3	28.8	31.8	29.2
SD	18.4	13	10.9	7.8
Inter-TC				
Mean	50.7	20.5	24.7	20.7
SD	20.1	10.9	13.9	5.4
Inter-REMSD				
Mean	44.8	32.8	31	20.2
SD	25.3	8.7	7.2	7

exposed to a CC, REMSD, or TC condition, tested on the four-component VI 15-s procedure, and returned to its daily training routine on the VI 15-s reinforcement schedule until stability was again achieved. Once the sequence of condition exposures on the VI 15-s schedule was completed, the VI 30-s schedule was reinstated. Rats, thus, were once again exposed to daily sessions of the four-component VI 30-s reinforcement schedule. Once baseline stability criterion was achieved ($M = 52.5$ sessions; range, 31 to 84), each rat was exposed to CC, REMSD, and TC conditions using the procedures previously described (see Table 1).

RESULTS

Figure 2 shows the responses per minute for each rat across baseline, CC (open circles), REMSD (solid circles), and TC (shaded circles) conditions and reinforcement schedules. Responses per minute are an average of each of the four 10-min components of the VI reinforcement schedule. Baseline data are the two sessions prior to each experimental manipulation and are summarized as the mean (solid line) and standard deviation (broken lines) in each phase. Each data point is a CC, REMSD, or TC test from a single session.

Response rates in baseline, CC, and TC conditions were similar across the VI 30-s and VI 15-s reinforcement schedules for R32, R33, and R41. Average response rates for R40 in baseline, CC, and TC conditions decreased across the three schedule manipulations. Rat

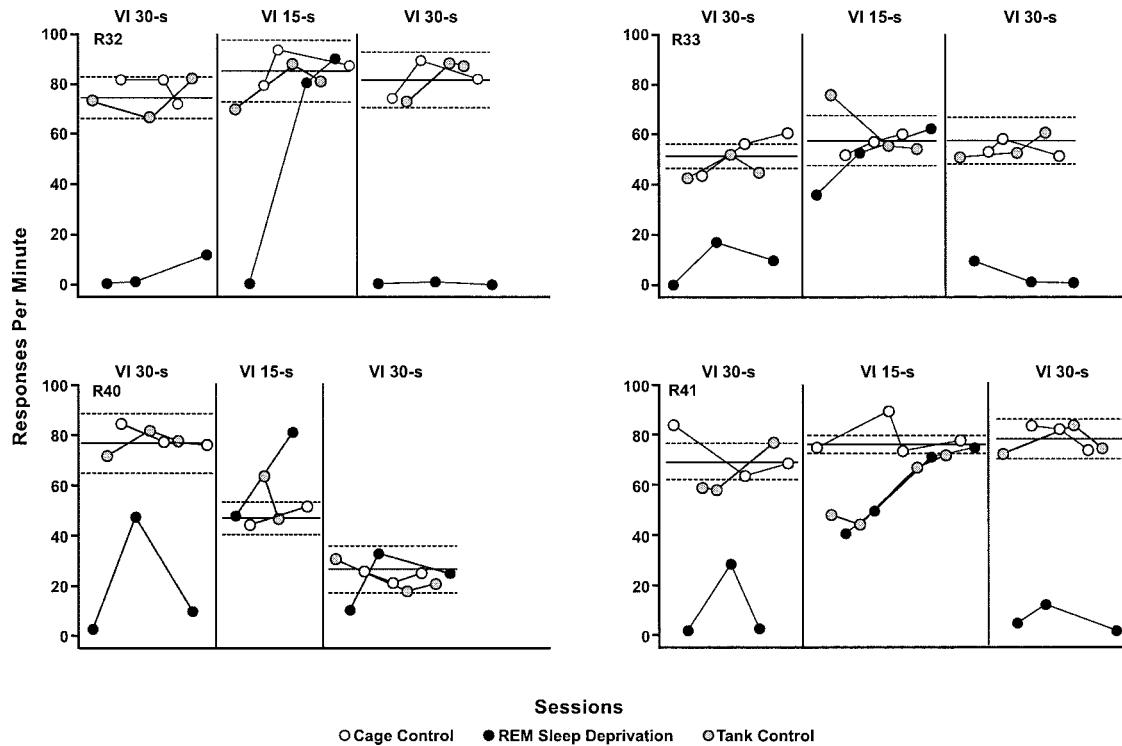


Fig. 2. The number of lever presses per minute for Rats 32, 33, 40, and 41. Data points are shown for sessions following exposure to cage control (CC) (open circles), rapid-eye movement sleep deprivation (REMSD) (closed circles), or tank control (TC) (shaded circles) conditions. Baseline data are summarized in each phase (i.e., VI 30 s, VI 15 s, and VI 30 s) as mean (solid line) and standard deviation (broken lines). Data are presented in the order in which rats were exposed to the CC, REMSD, and TC conditions.

R41 responded at lower rates following the first two TC exposures, but this proved temporary in subsequent post-TC test sessions. REMSD decreased lever pressing during the initial VI 30-s phase for each subject.

When the schedule was changed to VI 15 s, in the post-REMSD test sessions response rates either increased above VI 30-s levels in the first VI 15-s test session (R33 and R40) or response rates increased across successive exposures to the REMSD conditions (R32 and R41). For R32, R33, and R41 a return to the VI 30-s phase and exposure to REMSD decreased responding. The lever presses of R40 post-REMSD (VI 30 s) returned to the level observed in the previous VI 30-s condition, but because of the decline in this rat's response rate across conditions, no effect of REMSD could be detected.

Figure 3 shows the food pellet deliveries per minute across baseline, CC (open circles), REMSD (solid circles), and TC (shaded

circles) conditions and reinforcement schedules. Food pellet deliveries are an average of each of the four 10-min components of the VI schedule. Baseline data represent the two sessions prior to each experimental manipulation and are summarized as the mean (solid line) and standard deviation (broken lines) in each phase.

Food pellet deliveries were decreased by REMSD in the initial VI 30-s phase but increased across repeated REMSD exposures. Food pellet deliveries were unaffected by REMSD during the VI 15-s phase (with the exception of R32's performance following the initial REMSD exposure). As with lever pressing, food pellet deliveries decreased for R32, R33, and R41 during the second VI 30-s phase and REMSD exposure, with no increasing or decreasing trend present. Food pellet deliveries for R40 were consistent with baseline levels.

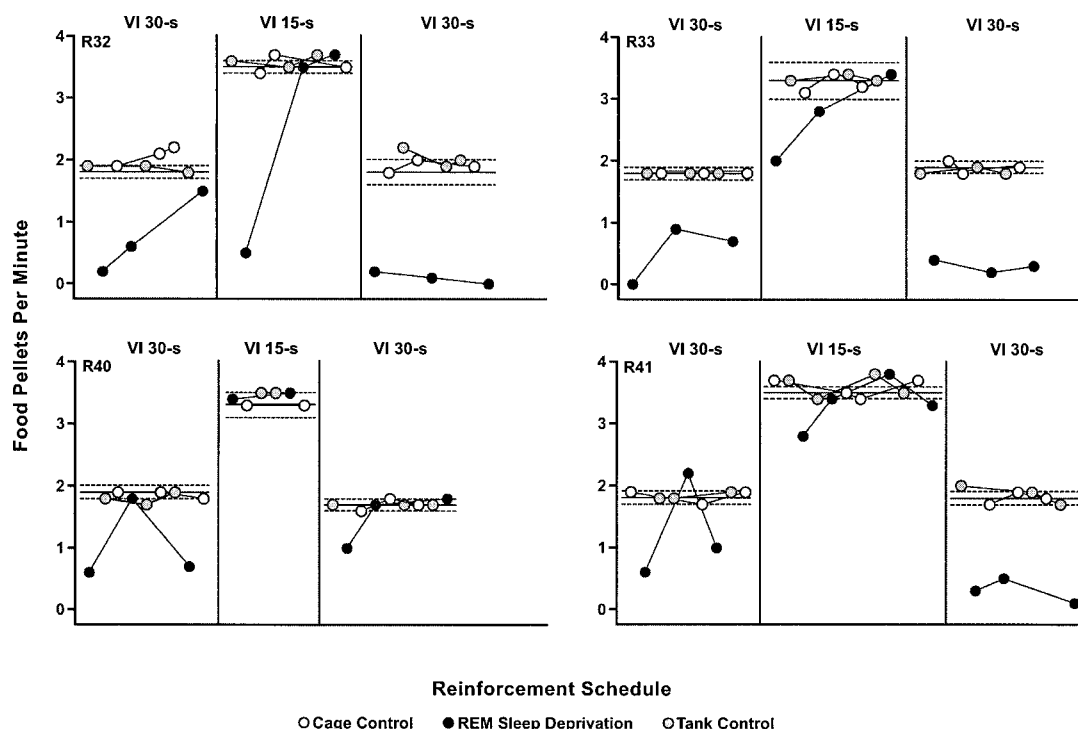


Fig. 3. The number of pellets earned per minute for rats 32, 33, 40, and 41. Data points are displayed for sessions following exposure to cage control (CC) (open circles), rapid-eye movement sleep deprivation (REMSD) (closed circles), or tank control (TC) (shaded circles) conditions. Baseline data are summarized in each phase (i.e., VI 30 s, VI 15 s, and VI 30 s) as mean (solid line) and standard deviation (broken lines). Data are presented in the order in which rats were exposed to the CC, REMSD, and TC conditions.

DISCUSSION

The effects of sleep deprivation on lever pressing and food pellet deliveries varied as a function of the schedule value. In seven of eight VI 30-s conditions, rats responded at lower rates following 96 hr of REMSD than following control conditions in which they were not sleep deprived. When the rate of reinforcement was increased by changing to a VI 15-s schedule, response rates in the post-REMSD sessions generally exceeded those maintained by the VI 30-s schedule. This effect was reversed for 3 of 4 rats when the VI schedule was returned to 30 s. When rats were exposed to the CC and TC control conditions, no systematic changes in behavior were observed relative to baseline. These results suggest that the length of a VI reinforcement schedule influences response rates following 96 hr of REMSD.

These findings extend an understanding of the effects of REMSD on food reinforced responding by showing that the effects of sleep

deprivation can be influenced by reinforcer rate. In a previous experiment, Kennedy (2002) maintained responding on a multiple FR 30 FI 60-s reinforcement schedule. This procedure established two distinct response and reinforcement rates. On average, subjects responded at 130 responses per minute (two reinforcers per minute) during the FR component and 40 responses per minute (one reinforcer per minute) during the FI component. Responding initially decreased when rats were exposed to 96 hr of REMSD, but this effect was temporary. In the current experiment, responding initially was maintained on a VI 30-s reinforcement schedule that established response rates in the range of 50 to 80 responses per minute (two reinforcers per minute). Response rates were consistently decreased following REMSD. When the VI schedule value was changed to 15 s, response rates in the control sessions did not change for 3 of 4 rats, but reinforcement rates doubled (see Figure 3). Responding on

the VI 15-s schedule was less disrupted by REMSD than was responding on the VI 30-s schedule. The current findings show that reinforcer availability can moderate the effects of REMSD. In our previous research (Kennedy, 2002), the relation between sleep deprivation and reinforcer availability was confounded because of the multiple schedule used and differing response rates that were generated. The current findings suggest a role for reinforcement availability in influencing the behavioral effects of sleep deprivation.

These findings suggest that food deprivation and sleep deprivation interact, and, at certain relative levels of deprivation, one operation successfully establishes one consequence (e.g., sleep) as more reinforcing than another (e.g., food). For example, in baseline and control sessions, rats had *ad libitum* access to sleep, but were food deprived. Under these conditions, response allocation shifted to lever pressing presumably because the establishing operation for food renders pellets a more effective reinforcer than sleep, given that sleep access may be conceptualized as an abolishing operation (rendering sleep a functionless behavioral consequence). If, however, access to sleep is restricted, the establishing operation associated with sleep deprivation may result in a shift in response allocation away from responding for food to sleep. In both the current and previous investigations, 96 hr of REMSD seems to be a point at which shifts in response allocation occur in relation to our food restriction procedures.

The current results suggest, in addition, that VI schedule value (programmed schedule rate) may interact with sleep deprivation to determine rates of food-maintained behavior. One way of conceptualizing this effect is to consider the availability of food across VI schedule values. Following sleep deprivation, when food availability was relatively high (i.e., VI 15 s), response allocation shifted toward lever pressing rather than sleep. When food availability was relatively low (i.e., VI 30 s), response allocation apparently shifted toward sleep in sleep-deprived subjects. It appears that increasing the rate of food reinforcement moved choice toward lever pressing and away from alternative behavior.

The effect of REMSD on food-reinforced

behavior does not appear to be a result of a change in the value of food as a positive reinforcer (see Kennedy, 2002). In Kennedy's Experiment 2, sleep deprived rats were tested in an operant chamber that did not permit access to REM sleep. Under such conditions, rats continued to respond for food pellets at the same response rates suggesting that REMSD did not alter food as a positive reinforcer. Therefore, changes observed in the current experiment suggest that the option to sleep under REMSD conditions competes with lever pressing for food reinforcement under some, but not all, reinforcer availability conditions.

The effects of REMSD on food reinforced responding differ from those obtained for responding on free-operant avoidance schedules in other experiments. On schedules of free-operant avoidance, response rates increase following REMSD (Kennedy et al., 2000), whereas REMSD has a different effect on positively reinforced behavior (Kennedy, 2002). The current study further demonstrates that REMSD has distinct effects on positively reinforced responding that differ from previous findings for negatively reinforced behavior. In the case of negatively reinforced behavior, REMSD appears to act directly on behavior-environment relations by increasing the aversiveness of environmental events (May et al., 2003; Onen, Alloui, Eschaliere, & Dubray, 2000). Thus increases in avoidance responding following REMSD may be due to increased nociceptive behavior in avoidance contexts.

In summary, response rates were decreased by REMSD when behavior was maintained on a VI 30-s reinforcement schedule, but response rates were within baseline range following repeated REMSD exposures when behavior was maintained on a VI 15-s reinforcement schedule. These data suggest that the effects of REMSD interacted with the value of the VI reinforcement schedule to alter response allocation to food reinforcement. These findings show that the behavioral effects of sleep deprivation can be mediated by environmental events such as food reinforcement parameters.

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